

**ETHOLOGY OF *EUDIOCTRIA TIBIALIS* BANKS
(DIPTERA: ASILIDAE) IN MARYLAND:
REPRODUCTIVE BEHAVIOR**

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Abstract.—Precopulatory behavior in *Eudioctria tibialis* Banks consists of males making short darting flights from perch to perch in search of females with which to mate. Search flights and copulations are most common in sunlit clearings during mid-afternoons. Searching males attempt to copulate with conspecifics either in flight or while they rest on perches. Copulations occur in the tail-to-tail position, and are short, with most lasting less than 15 min. Females show varying degrees of receptivity, copulate several times, and produce eggs continuously throughout their adult lives. Eggs are laid singly at a number of locations. Eggs are described and reproductive strategies are discussed.

In the first paper in this series on the ethology of *Eudioctria tibialis* Banks (Scarborough, 1981a), correlations were made between certain diurnal behaviors and the time of day. Three discrete behaviors (foraging, mating, and perching) were identified. Each behavior was recorded per hour of the day in clearings at Loch Raven Watershed, Baltimore Co., Maryland. Proportions of individuals actively involved in each behavior were used as criteria to determine the asilids diurnal behavior pattern. Results showed that as one behavior decreased in frequency others increased. Feeding was more frequent soon after the asilids entered clearings and before they left in late afternoon (Scarborough, 1981b). Feeding rates decreased during mid-afternoon as reproductive behaviors increased. This paper reports the reproductive behavior of the species.

METHODS

General methods and techniques used in this study were described earlier (Scarborough and Norden, 1977; Scarborough, 1981a). Data of flight activities of males were obtained by observing an individual fly during the first 15 minutes of each hour (1000-1800) of the day. A different individual ($N =$

15) was selected at random for observation during each 15 minute period. Activities were recorded as searching flights (short-darting flights in search of receptive females), forage flights (flights made toward flying potential prey), or orientation flights (discrete flights from one perch to another in response to changing environmental conditions and subsequent reduction in prey activities or densities). Data on each behavior were arranged in two-hour blocks. General observations of copulation, oviposition, and related behaviors were taken during the 1972–76 summers. Some females ($N = 20$) were captured while copulating and retained for 24 hours in large glass containers in the laboratory. The deposited eggs were later counted and measured. Each female was then dissected and eggs with tanned chorions found within the oviducts were counted.

RESULTS AND DISCUSSION

Precopulation Behavior.—Scarbrough and Norden (1977) defined search flights of *Cerotainia albipilosa* Curran as short-darting flights made by males in search of receptive females with which to mate. These flights usually terminated in the vicinity of perched females where males landed on nearby perches or immediately began to exhibit courtship displays in front of females. Search flights were the only discernable activity associated with precopulation behavior exhibited by *Eudioctria tibialis* males.

Flights were similar to those described for *C. albipilosa* in that they were short (ca. 1–3 m), rapid flights over vegetation, and were often terminated at perches near conspecifics or other insects which exhibited similar body features. They differed in that the male remained perched for a short time (ca. 1–10 sec) before flying to another perch or attempting to copulate.

Males sometimes hovered momentarily in flight above perched insects or tall vegetation spikes without landing. Males of *Dioctria* spp. (Melin, 1923) and *C. albipilosa* (Scarbrough, 1978) have been reported to oscillate above perched conspecifics, other insects, and various objects, e.g. twigs, nails, leaf tips. It has been suggested that this is partly reflective of the asilids limited visual acuity. However, this behavior may be significant in terms of males locating receptive females with which to mate. In each observation where male *E. tibialis* hovered above perched insects ($N = 42$), the latter invariably flew with the male following. This "flushing behavior" may have selective value in that it could increase the frequency of male-female encounters.

Foraging and orientation flights differed from search flights in that males remained perched from longer periods between flights (Scarbrough, 1981a, b). Forage flights also differed from search flights in that pursuit was directed at a wide range of dissimilar flying prey rather than flying or perched conspecifics or similar appearing insects.

A two-by-four contingency table of flight activities arranged for four con-

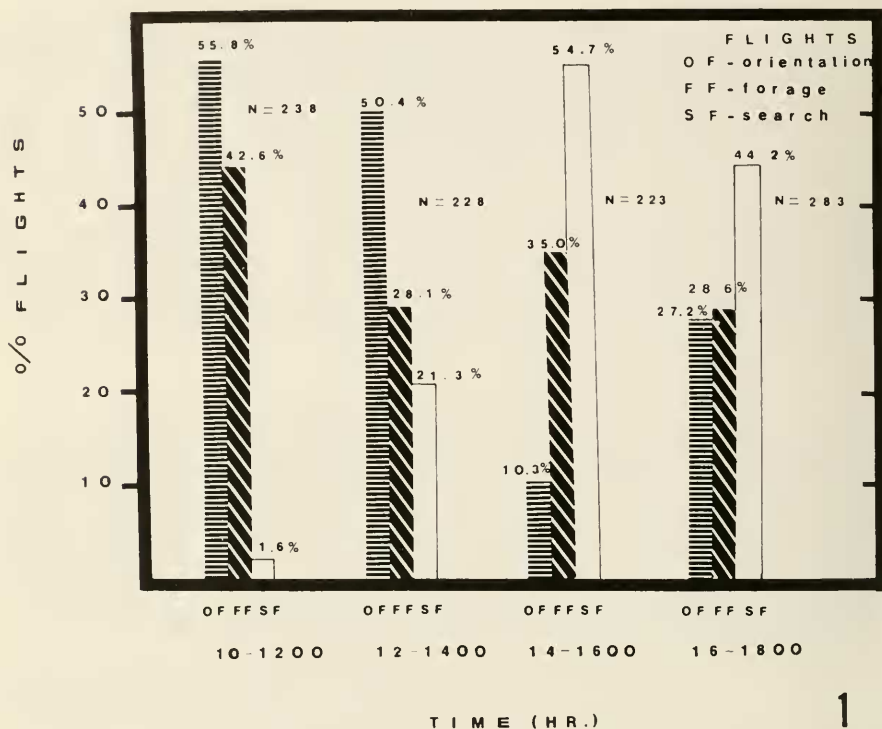


Fig. 1. Diurnal flight activities of male *Eudiectria tibialis* in sunlit clearings at the Loch Raven Watershed, Baltimore Co., Maryland.

secutive periods showed that as one activity decreased, other activities increased ($\chi^2 = 89.2$, $P < .001$; Fig. 1). Search flights occurred throughout the observation period, although they were more frequent during mid-late afternoon when flight activities associated with feeding and orientation had decreased. Similar responses have been reported for other asilid species (Dennis and Lavigne, 1975; Lavigne and Dennis, 1975; Musso, 1971, 1972; Scarbrough and Norden, 1977; Scarbrough, 1979; Scarbrough and Sraver, 1979).

Copulation.—While searching, males attempted to copulate with conspecifics either in flight or while they rested on perches. When females were encountered in flight, males followed and usually overtook them in flight where copulation was attempted. In some instances, males followed females to perches and landed on nearby perches. Occasionally males flew from their perches and attempted to copulate with the perched females. However, they usually remained perched until the females flew again. The males then followed them, overtaking them in flight. Males often followed females to several perches before attempting to copulate. In still other instances, males



Fig. 2. Copulating pair of *Eudiectria tibialis*.

"flushed" females from perches by hovering above them only to overtake them in flight or as they landed. Melin (1923) reported a similar behavior pattern where both *D. rufipes* DeGeer and *D. hyalipennis* Meigen oscillated above perched females. When the females flew, the males followed and often overtook them in flight.

A male attempted to mate as soon as a female was located. Copulation was initiated at perches when the male landed on the female's thorax (42.7%, $N = 495$). He quickly moved laterally to her pleuron, holding onto her legs, dorsum of the thorax and wings. He rotated his abdomen ca. 90° below that of the female's and probed at her genitalia. Sometimes the female fell on her pleuron in which case the male moved to her sternum. Union of their genitalia occurred as the two lay on their sides. However, most copulations (57.3%, $N = 495$) began when the male overtook the female in flight. The male grasped her wings and/or dorsum of the thorax. The grappling pair then fell to the ground or into vegetation where copulation ensued. Immediately following union of the pair's genitalia, the male moved behind the female into a straight line, assuming a tail-to-tail position (Fig. 2). The copulating pair then usually flew to another perch in the clearing, and remained quiet, not moving unless disturbed. The female initiated the flight, pulling the male behind her.

The copulating pair perched on a leaf with the female located at its tip

and in a position similar to that used for foraging (Fig. 2). The male was low in profile, with its legs spread more lateral than usual, and its weight distributed on all tarsomeres, which were in contact with the leaf surface. His wings were spread at an angle ca. $50-70^\circ$ to the long axis of its body, and his abdomen was curved down and under the female's genitalia. In contrast, the female stood higher in profile with the legs closer to her body and her weight distributed on the apical two or three tarsomeres. Her abdomen was straight, and wings were folded above her body.

Visible movements exhibited by the mating pair consisted of abdominal pumping, head movements and grooming. Both sexes frequently produced irregular peristaltic contractions, beginning at abdominal segment 5 or 6 and radiating posteriorly to the end of the body. Sometimes these waves were sufficiently strong to produce a rapid jerking motion of the abdomen. These movements were presumably associated with sperm transfer by males and, perhaps, the forcible movement of fluid into the spermatheca by females (Dennis and Lavigne, 1975). Both sexes were aware of movement and insects near them, but did not forage while copulating. They moved their heads quickly in the insects' direction as they passed. Head movements were more apparent and frequent with females than males and, presumably, were related to the position of the female on the leaf which gave her a wider field of vision. Females frequently (31.0%, $N = 184$) fed during copulation, although the prey were captured before copulation commenced.

Most attempts at copulation by males were unsuccessful, and in other cases, several attempts were made before copulation was accomplished. Females expressed varying degrees of non-receptivity by 1) moving their abdomens and genitalia away from the male's, and concurrently moving her legs and kicking vigorously at the male, 2) when free, the wings were vibrated, producing a low pitched buzzing sound, or 3) flew to new perches. In cases of immediate copulation, females remained passive, showing no obvious attempts to prevent copulation. Like many asilid species studied (Lavigne et al., 1978), *E. tibialis* females exhibited no clearly defined response, other than avoidance, to males prior to physical contact that would indicate either receptivity or non-receptivity.

Males also attempted to copulate with conspecific males and other insects, e.g. muscoid and conopid flies and bracionid wasps, which had similar body shapes and colors. Copulations were attempted with conspecific males in flight and on perches, whereas attempts to mate with non-asilids occurred at perches only. The latter could not be construed as foraging since all evidence concerning foraging behavior of *E. tibialis* indicated that the potential prey are flying and are usually smaller than the predator (Scarborough, 1981b). Apparently males cannot recognize an insect as a female until they have made physical contact.

A second male sometimes attempted to copulate with a copulating pair. The intruder landed on the perch, quickly grasping one member of the pair, usually the female. However, this response is not believed to be an indicator of recognition of a female, but rather it is more likely related to the usual position of a perched asilid on the tip of the leaf. The pair responded by moving to another area of the leaf, then kicking and finally flight to a different area of the study site when the intruder continued the disturbance. In one instance, a mating male released his grasp on the female, and the intruding male quickly clasped the female's genitalia and copulated with her. The female remained quiescent during the entire episode.

Copulations were usually short ($\bar{x} = 13.6$ min, $N = 50$) ranging between 3 and 55 minutes. Thirty-five (70%) copulations lasted less than 15 minutes. These data agree with those reported for other species in the Dasypogoninae (Dennis and Lavigne, 1975).

Separation ($N = 42$) was usually initiated at the perch by the female, kicking the male with her hind legs. He would then release her genitalia, and fly immediately to a new perch. In many instances he left ($N = 21$) the clearing. The female groomed her abdomen or genitalia, and flew ($N = 44$) to another perch in the vicinity or foraged. Only 6 females flew from the clearing following copulation. In a few cases, no noticeable signal was detected to indicate cessation of copulation. The male released his grasp on her genitalia and flew away. Conversely, the female remained perched for a few seconds and then foraged toward a passing insect.

A few species of asilids have recently been reported (Scarbrough, 1968; Bullington and Lavigne, 1980; Lavigne et al., 1980) to mate several times. *Eudioctria tibialis* behaved similarly with some females copulating with two or more males. Four marked females copulated with two different males during one afternoon and a fifth with three males. Males were not observed to mate with several females, although they undoubtedly do copulate several times. Males frequently attempted to copulate with other females immediately following separation from another.

Figure 3 shows the proportion of copulating pairs found in clearings during an eleven hour day for 15 days in 1976. Mating pairs were more common between 1300 and 1500 hrs, which corresponds to periods when males were most abundant in clearings and when foraging-feeding activities were low (Scarbrough, 1981a).

Oviposition Habits.—The method used by an asilid to deposit eggs is directly correlated with the degree and type of specialization of the female ovipositor (Melin, 1923). The ovipositor of *Eudioctria* spp. (Adisoemarto and Wood, 1975) in general, and *E. tibialis* (Scarbrough, unpublished data) specifically, lacks specialization for digging into or penetrating substrates into which to deposit eggs. This suggests that *E. tibialis* drop their eggs

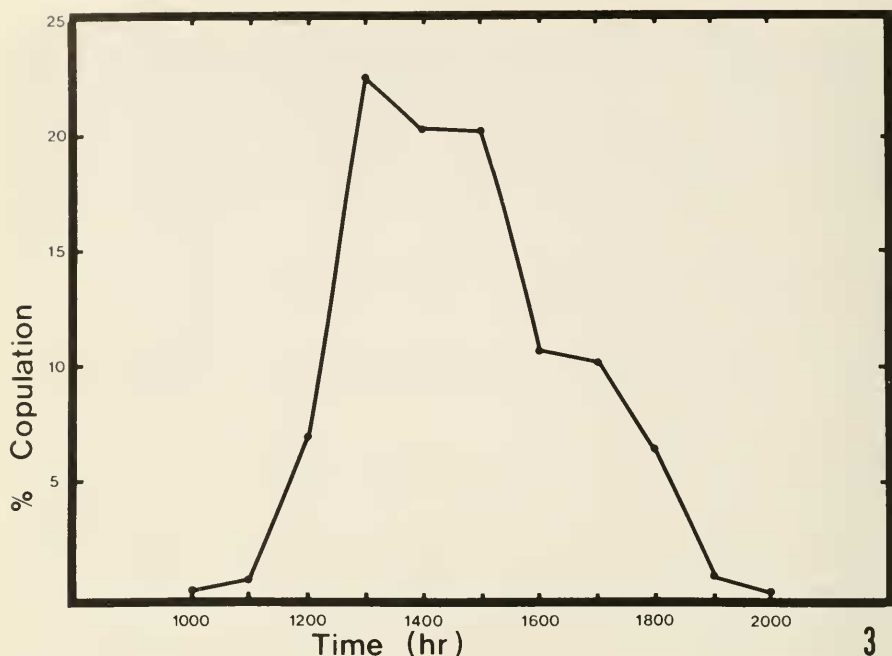


Fig. 3. Proportion of copulating pairs of *Eudiectria tibialis* in sunlit clearings during an eleven hour day per day in the Loch Raven Watershed.

either in flight or deposit them on substrates. Field observations support this hypothesis. Three females were observed depositing eggs. One female flew to perches on three different plants. At each perch, she arched the apex of the abdomen slightly downward and touched its end to the leaf surface. A slight peristaltic contraction was produced at the tip of the abdomen and was followed by the release of an egg which fell to the ground. The female then groomed the abdomen and genitalia and flew to a new location. A second and third female were found ovipositing while perched on exposed, loose sandy soil along a footpath and on the ground below sparsely spaced vegetation, respectively. Both females repeated the above behavior pattern. An egg was recovered at each site.

At least four European species of *Diectria* (*hyalipennis*, *rufipes*, *atricapilla* Meigen, *oelandica* L.) possess similar ovipositors and oviposition habits (Melin, 1923). Females fly from perch to perch in their respective habitats, land on vegetation or leaf layer on the forest floor, and drop eggs singly at each site.

The total number of eggs produced by an asilid is difficult to determine by direct observation or by dissection (Melin, 1923). Field observations

suggest that gravid females of *E. tibialis* deposit eggs singly at a number of locations per day. Females ($N = 20$) captured (1100–1200 hrs) late in the fly season and placed in 256 dram glass containers deposited 6 to 30 ($\bar{x} = 12.1$) eggs within 24 hours. Dissection of these females revealed that they possessed a large number of eggs (<50) in their genital tracts, representing various stages of development. The common oviducts of all females dissected contained 2 to 13 ($\bar{x} = 6.0$) eggs, which were indistinguishable in size and color of their chorions from those deposited in the field. The lateral oviducts also contained several eggs of equal size, although their chorions were lighter in color. Furthermore, females dissected shortly after the beginning of the fly season (Scarborough, 1981a) lacked eggs in their oviducts, and none of the eggs in the ovaries had tanned chorions (Scarborough, unpublished data). These preliminary results suggest that 1) egg production continues throughout the life of an adult female *E. tibialis*, 2) a small number of eggs are deposited per day, and 3) deposition of eggs is delayed for some period after emergence, because time and nutritional requirements are necessary for their development.

Eggs.—The eggs of *E. tibialis* are oval with one end more pointed than the other (Fig. 4). The chorion is highly sclerotized, reddish brown and possesses elevated facet-like (5–7 sided, $100\times$) ridges. At least four other genera have species that produce eggs with ridges on their chorions (*Holcocephala*, Dennis, 1979; *Cerotainia*, Scarborough, 1978; *Laphria* and *Dioctria*, Melin, 1923). These ridges face away toward the pointed end, forming a smooth surface. The pointed end has a lighter color than the surrounding chorion, and it contains the micropyle ($300\times$) at its center. The lighter color is probable related to the thinness of the chorion of this area, which is more easily broken than other areas of the egg surface. This end is probably the location (operculum) where a larva ecdyses from the egg. Eggs are uniform in size ($N = 200$, 10 from each of 20 females; $\bar{x} = 0.53$ L $\times$ 0.44 mm W; R = 0.50–0.56 mm L, R = 0.42–0.48 mm W).

Reproductive Strategies.—Scarborough (1981a) reported earlier that adults of *E. tibialis* were attracted to natural or artificial disruptions (clearings) in the forest canopy initially by localized prey aggregations and later by males searching for females with which to mate. The first movement into sunlit clearings produces a temporary aggregation in which females are slightly more abundant than males. Later in the day, males become more abundant than females as they replace foraging-feeding for searching-copulation behaviors. Males leave one clearing and fly to another as the density of receptive females decreases.

Female remain in clearings during most of the day insofar as prey densities are adequate and/or when physical-climatic conditions do not restrict predator-prey activity (Scarborough, 1981a, b). Upon leaving a clearing, females move to the forest canopy where they remain until conditions return to

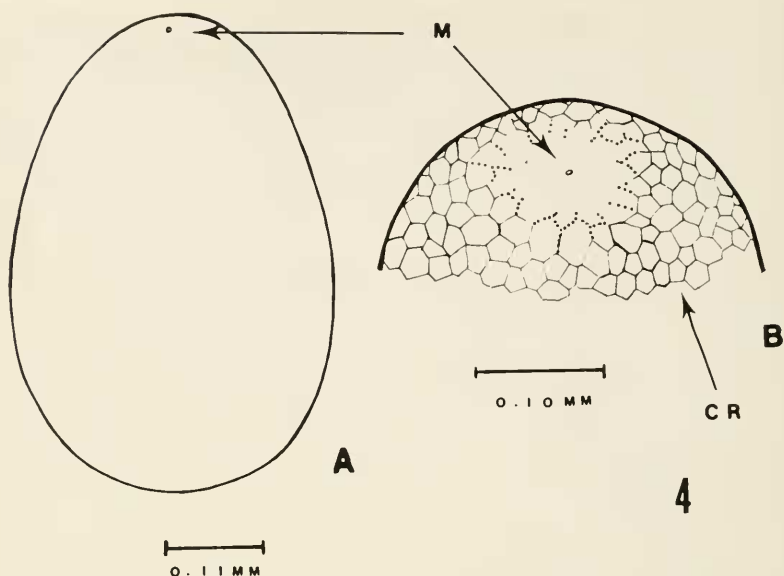


Fig. 4. Egg of *Eudioctria tibialis*. A, Shape of egg; M = micropyle. B, Chorionic ridge pattern (CR) which grades into a smooth surface surrounding micropyle.

optimum. They then either return to the same clearing or move to another. The selective advantage of remaining in clearings with optimal food resources for long periods permits greater energy expenditures for egg production rather than for increased flight in areas where resources are more dispersed. It also permits a greater opportunity for male-female contact in that females are basically stationary (Scarborough, 1981a) and, thereby, males can more readily locate them. If females were moving into and out of clearings as frequently as males in mid-afternoon, males would undoubtedly expend a greater amount of energy in order to locate them.

Foraging females in clearings will mate with several males during their adult lives. Because female *E. tibialis* produces eggs continuously during her life, with only a few maturing each day, the sperms she receives during one copulation are insufficient to fertilize all the eggs that she will produce. In this case, multiple copulations are advantageous in that they maximize genetic variability through copulation with several different males. However multiple copulations may be costly in that they occupy time that could be spent foraging (Alcock, 1980). Furthermore, because of clumped distribution of resources (localized prey concentrations) in the forest, a female may find it difficult to locate adequate prey resources for egg production in other areas where resources are less than optimal. In clearings where prey densities are more optimal, she may be forced to submit to short copulations and, yet, obtain adequate food resources.

The absence of an adequate quantity of viable sperms or some factor(s) associated with it in the spermatheca enhances multiple copulation (Manning, 1962a, b). Transfer of an adequate supply tends to temporarily inhibit multiple copulation, e.g. suppressing female receptivity. The data presented herein suggest that *E. tibialis* copulates several times during their lives and, sometimes, two or more times per day. It is probable that when a female copulates two or three times during one day, it is because of an insufficient quantity and/or quality of sperms transferred at a single copulation. Additional copulations then follow until the sperm supply in the female's genital tract rises to a point that it inhibits copulation. Copulations then cease until the sperm level falls below a minimum threshold, and subsequent internal factor(s) remove the inhibition.

Upon leaving clearings in late afternoon or during inclement weather, females may disperse to other clearings where their eggs could be more widely deposited throughout the forest. This behavior would decrease competition for larval developmental sites and increase the possibility of success of their progeny.

Like many species of bees, males of *E. tibialis* maximize their access to females through "scramble-competition." Males move into clearings where females are feeding and attempt to copulate with them as soon as possible to exclude competitors. The males' reproductive success is based solely upon their ability to locate potential females before their competitors do (Alcock, 1980).

In multiple copulation systems, the last male to copulate with a female prior to oviposition is the one that fertilized all or most of the eggs deposited at the next oviposition (Parker, 1970). Receptive females of *E. tibialis* copulate repeatedly accepting any male that can grasp them until an adequate sperm supply is obtained. Males which enter clearings with females early in the day have a maximum sperm supply. Because they have not copulated since the previous day, these males are more likely to transfer a sufficient amount of sperms to their mates, producing an inhibition of the mating process. This stimulates non-receptivity in the females and insures fertilization of her mature eggs with his sperms.

As the day progresses more and more males enter clearings and join the scramble for mates. The new arrivals originate from areas in the Watershed where receptive females were absent. The proportion of copulations increases in early afternoon, corresponding with the time of the rapid increase of males in clearings. In mid- to late afternoon, the proportion of copulations decreases, indicating that most females have copulated and received sufficient sperms to inhibit future copulations. Conversely, some females remain receptive because they received insufficient sperms or receptivity has been restored through removal of inhibition via oviposition. Thus, receptive females in mid-late afternoon contain sub-threshold levels of sperms. Males with sperms that locate these females are at a selective advantage. Fewer

sperms are needed to inhibit future copulations at this time of day than earlier. Therefore, these males contribute more genetically to succeeding generations than others.

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NOTE

Synonymical Notes on New World Bruchidae (Coleoptera), and an Emendation

J. Decelle called my attention to an error in our recent publication "Revision del genero *Megacerus* (Coleoptera: Bruchidae)" (Teran, A. L. and J. M. Kingsolver. 1977. Opera Lilloana 25: 1–287), p. 103. The citation "*B[ruchus] pygidionotatus* Pic, 1929, p. 36" under *Megacerus lunulatus* (Pic) should be corrected to "*Pachybruchus pygidionotatus* Pic, 1952, p. 15," described from Peru (Échange, Vol. 68). The citation on p. 106 (Teran and Kingsolver) giving the type-locality is correct for *Pachybruchus pygidionotatus*.

Examination of the type-specimen of *Bruchus bipustulatus* Fabricius, 1801 (Syst. Eleuth. 2, p. 238) disclosed that this name is a senior synonym of *Megacerus* (*Pachybruchus*) *acerbus* Teran and Kingsolver, 1977: 143. NEW SYNONYMY, NEW COMBINATION.

The name *Amblycerus baracoensis* Kingsolver, 1970 (Trans. Am. Entomol. Soc. 96: 484) is hereby emended to *A. baracoensis*.

From examination of type-specimens, the West Indian *Amblycerus martorelli* Bridwell, 1944 (J. Agric. Univ. P.R. 27: 133) is a junior synonym of *Amblycerus sallei* (Jekel), 1855 (Insecta Saundersiana, p. 30). NEW SYNONYMY.

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